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INTERSPECIFIC AND INTERGENERIC RELATIONS BETWEEN NEMATODES PARASITIC IN THE STOMACHS OF KANGAROOS AND WALLABIES

by H. HOSTE* & I. BEVERIDGE†

Summary

HOSTE, H. & BEVERIDGE, I. (1993) Interspecific and intergeneric relations between nematodes parasitic in the stomachs of kangaroos and wallabies. *Trans. R. Soc. S. Aust.* **117**(4), 171-177, 30 November, 1993.

Associations between conspecific and confamilial nematodes co-occurring at high prevalences in the stomachs of the eastern grey kangaroo, *Macropus giganteus*, from Victoria, the red kangaroo, *M. rufus* from New South Wales and rock wallabies of the *Petrogale assimilis* species complex *P. assimilis*, *P. sharmani* and *P. mareeba*, from Queensland, were investigated using principal components analysis. A similar pattern of associations was found in each host species, consisting mainly of positive associations between nematode species. Negative associations were found with *Rugopharynx australis* the numerically dominant nematode in *M. giganteus* and *M. rufus*, and to a lesser extent with *R. zeta* in *Petrogale* spp. The complex nematode communities present in each host were shown to be stable, with few negative associations between members.

KEY WORDS: *Macropus giganteus*, *Macropus rufus*, *Petrogale assimilis*, nematodes, communities, associations, multivariate analysis

Introduction

Parasite communities in homeothermic animals are frequently complex in nature, with many species of parasites occurring in an individual host or host organ (Bush *et al.* 1990; Kennedy & Bush 1992). Because of the complexity of the community and, frequently, the large numbers of helminth species involved, the question as to whether community members interact or have interacted in the past to produce a stable, predictable structure or are non-interactive and result from a random collection of independent, individual species, has received considerable attention (see Holmes 1986; Price 1986). Evidence for the existence of interactive communities has been provided in the case of cestodes of ducks (Bush & Holmes 1986 a,b) and trichostrongyloid nematodes in sheep (Diez-Banos *et al.* 1992; Hoste & Cabaret 1992) while at the other extreme, the complex assemblages of monogenean parasites present as ectoparasites of fishes appear to exhibit few interactions (Rhode 1979; Koskivaara & Valtonen 1992; Koskivaara *et al.* 1992).

Amongst nematode parasites, the best known examples of complex parasite communities existing within a single host organ are the oxyuroid nematodes of tortoises (Schad 1963; Petter 1966), and the strongyloid nematodes of elephants (Chabaud 1957), horses (Kennedy & Bush 1992) and kangaroos (Inglis 1971; Kennedy & Bush 1992). In the case of kangaroos, up to 40 species of nematodes, all belonging to a single order, the Strongylida, occur in the complex saccular fore-stomachs of individual host species (Spratt *et al.* 1990), with numbers of parasites reaching 300,000 or more (see Beveridge & Arundel 1979). Several studies (Mykytowycz 1964; Mykytowycz & Dudzinski 1965; Smales & Mawson 1978b; Arundel *et al.* 1979) have demonstrated that different species or genera of nematodes have different site preferences within the stomachs of kangaroos, as is the case with oxyuroid nematodes in tortoises (Schad 1963; Petter 1966), but there have been no studies undertaken to determine whether there is any evidence of interactions within these helminth communities.

Recently, Hoste & Cabaret (1992) have utilised a principal components analysis (PCA) and comparison with the model of Motomura (1947) in which the $\log_{10}$ abundance of a species is correlated with its rank in terms of abundance for examining the stability of nematode communities in sheep and the existence of interactions between the species or genera of parasites present with a host. In this paper, we apply their techniques to examine whether there is evidence of competitive interactions between the nematode parasites present in the stomachs of three taxa of macropodid marsupials.

Materials and Methods

Parasitological data

Data utilised in this study were obtained from earlier epidemiological studies on the parasites of macropodids.

The data for *Petrogale assimilis* included 35 specimens of *P. assimilis* as well as five specimens of what were formerly known as the Mt Claro and Mareeba chromosomal races of this species. They have recently been named *P. sharmani* and *P. mareeba* respectively (Eldridge & Close 1992). Rock wallabies were collected over an extensive area of northern and

* Institut national de la Recherche Agronomique, Nouzilly, France.
† Department of Veterinary Science, University of Melbourne, Parkville, Vic. 3052.

western Queensland (see Beveridge *et al.* 1989) during a study of the taxonomy of the hosts. Nematode taxa included in the study, their prevalence and mean intensity of infection are shown in Table 1. Any helminth species occurring outside the stomach, or at a prevalence of less than 10% e.g. *Cloacina similis*, *Coronostrongylus coronatus*, *Labiostrongylus bancrofti*, *Macropostrongylus petrogale* etc.) was not considered to be a core species (*sensu* Hanksi 1982) and was excluded from the statistical analyses. In addition, nematodes such as *Woodwardostrongylus obendorfi* for which intensity data were not available, were also excluded. Since similarity coefficients for the helminth communities in *P. assimilis*, *P. sharmani* and *P. mareeba* are high (Beveridge *et al.* 1989), combination of their data was considered justifiable.

Data from *Macropus giganteus* were derived from an epidemiological study conducted at Yan Yean, Victoria, in which two adult and four juvenile kangaroos were collected at six-weekly intervals over a period of 10 months (Arundel *et al.* 1990). The prevalence and mean intensity of infection for the principal nematode species in the stomachs of these hosts are shown in Table 2. Any nematode species occurring in less than 10% of the host specimens (eg. *Alocostoma clelandi*) was excluded from the analysis, as were the species of intestinal cestodes.

Data on the helminth parasites of *Macropus rufus* were collected at a single locality, Menindee, New South Wales (see Arundel *et al.* 1979), with 12 animals collected every two months, over a period of two years. Samples of kangaroos were collected within Kinchega National Park and on properties immediately adjacent to the Park. The only difference in prevalence detected was in the case of the bile duct inhabiting cestode *Progamotaenia festiva* (see Arundel *et al.* 1979). No differences were detected in the intensity of infection with any parasite. Hence it was considered valid to use combined data from the two adjacent collection localities (Table 3). Helminth parasites occurring at a low prevalence or intensity, such as the nematodes *Macropostrongyloides* spp., and *Hypodontus macropi* and the cestodes *Progamotaenia ruficola* and *Triplotaenia undosa* were excluded from the analysis.

Changes in the nomenclature of parasites since the publication of the original epidemiological papers have been indicated in Tables 1-3, together with appropriate references. In *M. giganteus*, individuals of the genus *Labiostrongylus* and in *M. rufus* and *M. giganteus* members of the genus *Cloacina* were not identified in a quantitative fashion to species level, because of inadequate information on the taxonomy of these genera, though the species present at each locality were recorded. In *M. giganteus*, most of the species of *Cloacina* present are undescribed.

TABLE 1. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 39* Petrogale assimilis, P. sharmani *and* P. mareeba *from Queensland.*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx zeta (Johnston & Mawson, 1939)	53	2,190
Cloacina petrogale Johnston & Mawson, 1938	72	390
C. pearsoni Mawson, 1971	98	980
C. parva Johnston & Mawson, 1938	100	780
C. hydriformis Johnston & Mawson, 1938	46	200
Cl. sp. (undescribed) (*C.* sp. 1 of Beveridge *et al.* 1989)	54	420
Filarinema spp. (*F. dissimile* (Wood, 1931), *F. australe* (Wood, 1931), *F. mawsonae* Cassone & Baccam, 1985)	33	13

TABLE 2. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 45* Macropus giganteus *from Yan Yean, Victoria.*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx australis (Mönnig, 1926)	100	46,290
R. rosemariae Beveridge & Presidente, 1978	27	2,210
Cloacina spp. (*C. obtusa* Johnston & Mawson, 1939, *C.* cf. *hydriformis* Johnston & Mawson, 1938, *C.* cf. *elegans* Johnston & Mawson, 1938)	98	7,630
Labiostrongylus spp. (*L. bipapillosus* (Johnston & Mawson, 1938), *L. kungi* Mawson, 1955)	73	260
Pharyngostrongylus kappa Mawson, 1965	85	9,350
Strongyloides sp. (undescribed)	59	835

TABLE 3. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 100* Macropus rufus *from Menindee, New South Wales.*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx australis (Mönnig, 1926)	99	51,850
Wallabinema cobbi (Kung, 1948) (syn. *Zoniolaimus cobbi*)	84	9,655
Cloacina spp. (*C.* cf. *hydriformis* Johnston & Mawson, 1938, *C. expansa* Johnston & Mawson, 1939, *C. macropodis* Johnston & Mawson, 1938)	71	3,090
Labiostrongylus longispicularis Wood, 1931	88	332
Filarinema spp. (*F. flagrifer* Mönnig, 1929, *F. australe* (Wood, 1931))	92	79
Papillostrongylus sp. (undescribed) (= *P. labiatus* Johnston & Mawson, 1939 *sensu* Arundel *et al.* 1979)	41	1,580

Statistical methods

For each host species, a separate principal component analysis (PCA) was performed, using the STATITCF computer program (1988), on both the intensity data (*sensu* Margolis *et al.*, 1982) and the frequency data defined as the number of nematodes of a particular species expressed as a percentage of the total number of worms within that host. The data were standardised prior to analysis as (actual value − mean value for the variable) ÷ standard error for the variable.

The data were arranged in a correlation matrix whose columns (variables) were the parasite species and rows were the individual animals. Component axes were defined from correlations between the variables (parasite species numbers). The coordinates of each variable were then expressed in relationship to the new axes. Axes 1 to 3 were studied, the percentage of variability accounted for by each axis being indicated for each PCA in Table 4.

TABLE 4. *Percentage of total variability expressed by component axes 1, 2 and 3 following Principal Component Analysis (PCA) of the intensity and frequency of infection of* Petrogale spp., Macropus giganteus *and* M. rufus *with nematode parasites.*

Host species	Axis 1	Axis 2	Axis 3	Total (1 + 2 + 3)
Petrogale spp.				
Intensity	34.4	22.0	18.7	75.1
Frequency	31.6	23.8	19.2	74.6
Macropus giganteus				
Intensity	28.0	24.5	18.4	70.9
Frequency	33.6	21.3	18.3	73.2
Macropus rufus				
Intensity	37.0	19.7	16.8	73.5
Frequency	31.2	18.6	18.0	67.8

For each host species and each set of data, i.e. intensity and frequency, Euclidean distances between parasite species were calculated by applying Pythagoras' theorem to the coordinates of each variable, i.e. parasite species, was located within the three dimensional space constructed by axes 1 to 3 (Table 5). These distances characterised quantitatively the relation between nematode species. The minimum value for these distances was 0, the maximum 2. Distance values > 1.2 and < 0.8 are considered indicative of negative and positive interactions between species respectively (Hoste & Cabaret 1992).

In each host species, the distances between each pair of nematode species were calculated in the three planes and the result was called D_2. These D_2 distances were fitted to the logarithmic model of Motomura (1947) i.e. the decimal logarithms of distances were regressed on the rank of each species pair. According to Motomura's (1947) model, the $\log_{10}$ of the abundance of a species is correlated with its rank in the order of most abundant to least abundant species.

In addition, in order to represent the relation of one particular species to others present in the stomach, mean distances were calculated as the averages of the D_2 distances for each pair of worm species including the particular species of interest. These mean distances were called D_5 in both species of kangaroos as they were distances between a given parasite taxon and five others, and called D_6 in the case of the rock wallabies since the distance was from six other taxa.

TABLE 5. *Coordinates of nematode species on component axes 1, 2 and 3 following a Principal Components Analysis (PCA) performed on the intensity and frequency of infection of* Petrogale spp., Macropus giganteus *and* M. rufus, *with nematode parasites.*

Host	Parasite	Intensity Data Axis 1	Intensity Data Axis 2	Intensity Data Axis 3	Frequency Data Axis 1	Frequency Data Axis 2	Frequency Data Axis 3
Petrogale spp.	*Cloacina sp.* 1	-0.625	0.311	0.497	0.382	0.070	0.772
	C. hydriformis	-0.218	-0.813	-0.084	-0.338	-0.768	0.124
	C. parva	-0.783	0.298	-0.448	-0.629	0.501	-0.453
	C. pearsoni	-0.863	0.179	-0.394	-0.743	0.319	0.409
	C. petrogale	-0.456	-0.785	0.137	-0.224	-0.838	-0.248
	Rugopharynx zeta	-0.636	-0.081	0.505	0.912	0.039	-0.112
	Filarinema spp.	-0.024	0.198	0.653	0.349	0.120	-0.538
Macropus giganteus	*Rugopharynx australis*	0.653	0.594	0.169	0.954	-0.244	0.051
	P. kappa	-0.305	0.262	0.673	-0.109	0.876	-0.220
	Cloacina spp.	-0.374	0.714	-0.294	-0.906	-0.248	0.039
	Labiostrongylus spp.	-0.370	-0.077	0.688	0.076	0.614	0.450
	R. rosemariae	-0.517	0.647	-0.135	-0.444	-0.120	0.582
	Strongyloides sp.	0.785	0.337	0.216	-0.264	-0.010	-0.710
Macropus rufus	*Labiostrongylus longispicularis*	0.004	0.391	0.878	0.162	-0.088	0.622
	Filarinema spp.	-0.686	0.060	0.014	-0.487	-0.844	0.141
	Rugopharynx australis	-0.900	-0.133	0.087	0.988	0.037	-0.132
	Cloacina spp.	-0.503	0.627	-0.019	-0.318	0.419	0.578
	Wallabinema cobbi	-0.819	-0.159	-0.167	-0.050	0.259	0.386
	Papillostrongylus sp.	-0.138	-0.769	0.452	-0.728	0.393	-0.417

Results

Average distances of individual species from remaining species (D_5 and D_6)

Comparison of the mean euclidean distances for each worm species with related species in the three different hosts showed several similarities (Fig. 1). Firstly, in the three host species, the mean distances calculated from the frequency data were generally higher than those calculated from the intensity data. Secondly, no mean distances calculated from intensity or frequency data exceeded 1.2 which is suggestive of no negative association between species. Thirdly, based on the frequency data, the highest values of D_5 were associated with the species *Rugopharynx australis* in both of the kangaroo species. Though not so marked, a similar situation prevailed with *R. zeta* in rock wallabies having a D_6 value as high as any other of the other associations.

Average distances between species pairs (D_2 distances)

Comparison of the ranked D_2 distance distributions in the three host species added to the results obtained by analysis of the D_5 and D_6 distances. In the PCA performed on the frequency data (Fig. 2), the rank distribution of the D_2 distances for the 15 pairs of worm species in the red and grey kangaroos, and for

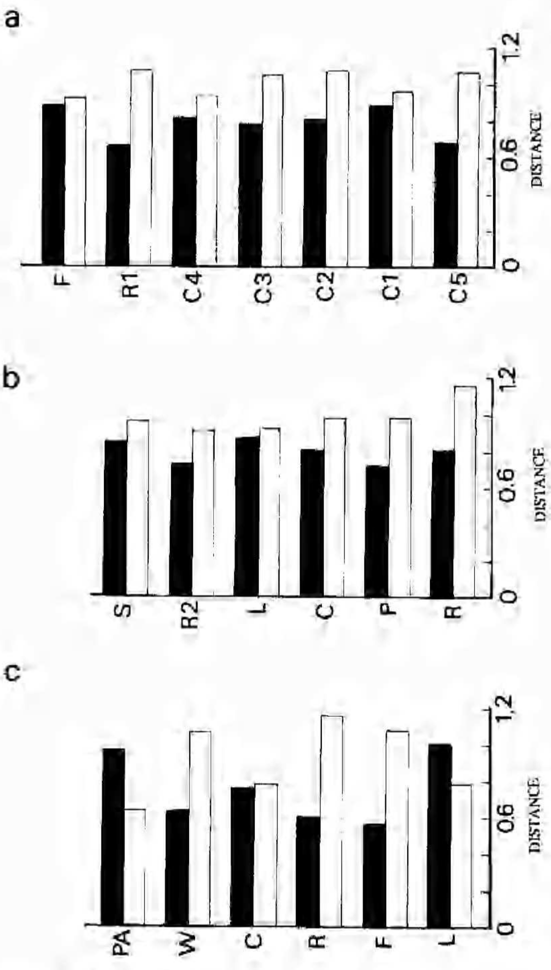

Fig. 1. Mean distances (D_5 & D_6) between individual parasite taxa, based on both intensity (closed histograms) and comparative frequency of occurrence (open histograms) in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis (PCA).

Legend: C, *Cloacina* spp.; C1, *Cloacina hydriformis;* C2, *C. parva;* C3, *C. pearsoni;* C4, *C. petrogale;* C5, *C.* sp.; F, *Filarinema* spp.; L, *Labiostrongylus* spp.; PA, *Papillostrongylus* sp.; P, *Pharyngostrongylus kappa;* R, *Rugopharynx australis;* R1, *R. zeta;* R2, *R. rosemariae;* S, *Strongyloides* sp.; W, *Wallabinema cobbi*.

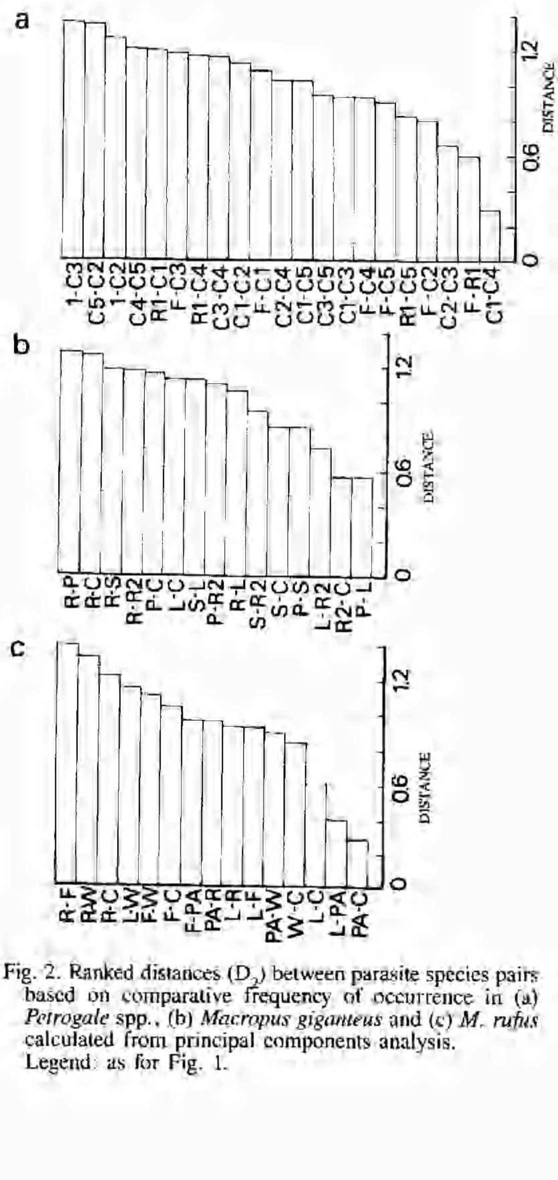

Fig. 2. Ranked distances (D_2) between parasite species pairs based on comparative frequency of occurrence in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis.

Legend: as for Fig. 1.

the 21 pairs in the rock wallabies fitted Motomura's model. Additionally, some of the distances between nematode species were high (> 1.2) which suggests negative interactions. This observation was made in the three different host species, and among those pairs exhibiting the highest distance values, *Rugopharynx* spp. were usually present. These results suggest that *Rugopharynx* was negatively associated with the other worm species based on the frequency analysis.

The D_2 distances calculated from the intensity data (Fig. 3) were lower than those obtained from PCA performed on the frequency data. In the three different host species, the D_2 distances were less than 1.2, and usually less than 1.0, which tends to indicate the lack of any significant negative association between nematode species. The rank distribution of patterns of these D_2 distances also fitted Motomura's model. When compared to the distribution of the D_2 distances obtained from the frequency analysis, the order of the different pairs in the intensity data was distinct, with a less well defined ranking of *Rugopharynx australis*.

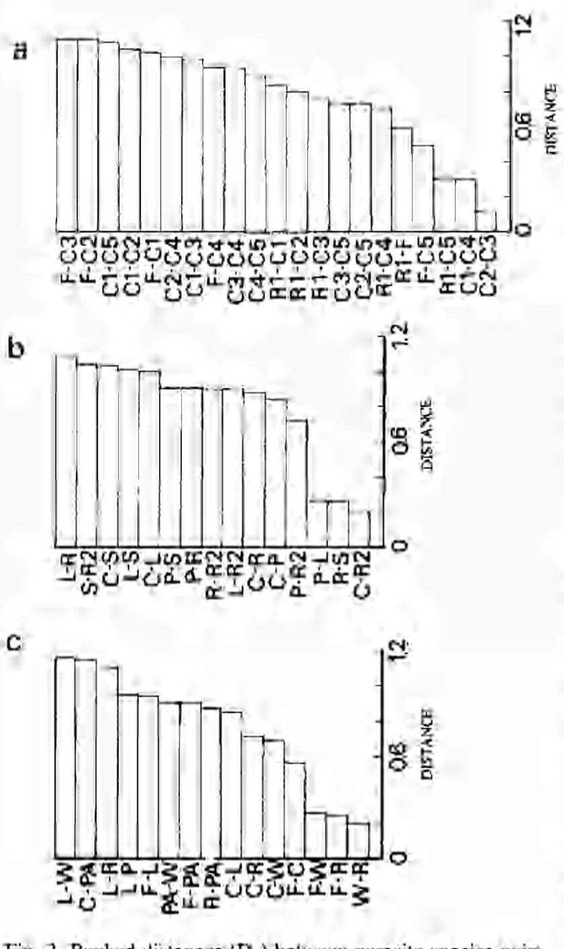

Fig. 3. Ranked distances (D_2) between parasite species pairs based on intensities of infection in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis.
Legend: as for Fig. 1.

Discussion

The results of analysis both of frequency and intensity of infection data for all three species of macropodid hosts can be fitted to Motomura's model (1947) for density associations between populations of similar species within the same biotope and suggest the existence of stable nematode communities in the stomachs of the macropodid species examined. Furthermore, most of the D_2 distances calculated on the intensity data were less than 1.0 and even less than 0.8. As these distances are thought to reflect the intensity of parasitism at the suprapopulation level or host population level, this fact provides additional evidence of the preponderance of positive associations between component species and hence infers the existence of stable communities. Positive associations are known to occur in the case of other host groups acquiring their parasite infections from grazing pastures contaminated with various species of infective third stage larvae of nematodes such as ruminants (Diez-Banos *et al.* 1992; Hoste & Cabaret 1992). On the other hand, the frequency-based distances mainly reflect the infracommunity present in the individual host, and the fact that the frequency-based distances were generally greater than those derived from intensity data suggests that additional regulatory factors are involved at the suprapopulation level, as occurs also in the case of ruminants (Hoste & Cabaret 1992). The regulation of nematode populations in kangaroos is not well understood. Smales & Mawson (1978) and Arundel *et al.* (1990) demonstrated that in the case of the Tammar wallaby, *M. eugenii* and eastern grey kangaroo *M. giganteus*, in winter rainfall areas of South Australia and Victoria, there was an increase in the number of nematodes present in the stomach during the moist winter months which is the most favourable period of the year for larval development in the external environment. Arundel *et al.* (1990) also demonstrated an effect of host age on certain species of nematodes (e.g. *Rugopharynx rosemariae*), with juvenile animals exhibiting a higher prevalence and intensity of infection, while in other nematode genera (*Cloacina*, spp., *R. australis*) intensity was higher in adult hosts. By contrast, the study by Arundel *et al.* (1979) on the red kangaroo, *M. rufus*, in the arid, non-seasonal rainfall region of western New South Wales indicated in the case of several of the dominant nematode species (*R. australis*, *Wallabinema cobbi*) that there was no seasonal effect on intensity of infection and that intensity of infection increased linearly with host age. In all of these three *Macropus* species, *Labiostrongylus* spp. exhibited an unique pattern of development, with larval stages maturing over a period of several months during the summer (Mykytowycz & Dudzinski 1965; Smales & Mawson 1978a; Arundel *et al.* 1979). Because of the lack of detailed knowledge of the way in which nematode populations in kangaroos are regulated, it is difficult to explain what the additional regulatory factors at the suprapopulation inferred by the present analysis might be. However, Petter (1966) also found an effect of host age and season on interactions between the oxyuroid nematodes of tortoises, suggesting that these might be general phenomena.

In contrast to other studies on gastro-intestinal strongylid nematodes (Hoste & Cabaret 1992; Diez-Banos *et al.* 1992), analysis of populations of the stomach-inhabiting nematodes parasitic in three species of macropodid hosts failed to reveal evidence of extensive negative interactions between nematode species. The only suggestion of negative associations involved *Rugopharynx australis* in red and grey kangaroos, and in both of these kangaroos, *R. australis* is numerically the dominant stomach nematode (Arundel *et al.* 1979, 1990; Beveridge & Arundel 1979). In the case of the rock wallabies no particular dominant species emerged. *Rugopharynx zeta* occurred at a higher intensity in rock wallabies than other gastric nematodes, but occurred at a prevalence of only 50%. *Cloacina pearsoni* and *C. parva* by contrast occurred in 100% of the hosts examined but at a lower intensity. The differences in intensity and prevalence may counteract one another to present a community in which there are few negative interactions. An additional consideration when comparing data from rock wallabies with that from the kangaroos is that in the former case, hosts were collected over a wide area of northern Queensland, compared with single localities for each of the kangaroo species.

Negative associations are evident in the frequency data only, which refers essentially to the infrapopulation at the individual host level: there is no such evidence from analysis of the raw intensity data, which relates to the parasite suprapopulation or the host population level. However, Holmes (1986) has cautioned that interactions are frequently obscured when suprapopulations are considered and that the optimum method for detection of interaction is at the infrapopulation level, a conclusion which is clearly supported by the current results.

Thus, the nematode communities present in the three species of macropodids examined here demonstrate similar features in being stable, and probably mainly non-competitive communities, with the exception of *Rugopharynx australis*. This lack of negative associations contrasts sharply with the results of Bush & Holmes (1986a) from studies on the cestodes of ducks and those of Hoste & Cabaret (1992) and Diez-Banos *et al.* (1992) for ruminants. Rohde (1979) suggested that in non-interactive communities not all niches are filled, there is no basis for competition and differential localisation of parasites occurs because it facilitates reproduction rather than minimises competition. Rohde's hypothesis (1979) is therefore consistent with the data currently available for nematode communities parasitic in the stomachs of macropodids. The kangaroo stomach is a relatively enormous organ in comparison with the size of parasites, and data from various sources (e.g. Beveridge & Arundel 1979) suggests that healthy macropodids are capable of harbouring numbers of nematodes far in excess of those encountered in this study. Hence it is not unreasonable to assume that vacant niches are abundant within kangaroo stomachs, given the proviso that nematode numbers only have been examined, without any consideration of their relative biomass. Whether the differential localisations of nematodes observed are due to reproductive strategies or due to the presence of competition in the past, during the evolution of the parasite community structure, is not clear.

Price (1986) predicted that considerable variation in community characteristics might be expected when a sufficiently wide range of communities was examined. The present results indicate that speciose nematode communities of homoeothermic vertebrates, while stable in their structure, may not necessarily display significant negative associations between their component members.

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